

A comparison of anamorphs of some *Pachyphlodes* species and the type of *Chromelosporium*: are they congeneric?

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ABSTRACT—There is a question of whether or not the name *Chromelosporium* competes with the name *Pachyphlodes* given that both genera exhibit similar conidiogenesis. We address here the question through a comparative study of their anamorphs. The type specimen of *C. ochraceum* (generic type of *Chromelosporium*), has been studied and compared to newly collected specimens of two *Pachyphlodes* species, *P. nemoralis* and *P. citrina* (whose identity was confirmed through comparison of ITS DNA sequences) and an unidentified species from the *Pachyphlodes*–*Plicariella* lineage. Comparison of the morphology of the *Pachyphlodes*–*Plicariella* lineage anamorphs with *Chromelosporium ochraceum* reveals discriminating characters that may support a generic distinction.

KEYWORDS—Ascomycota, *Glischroderma*, *Pezizaceae*, molecular analyses

Introduction

Corda (1833) described *Chromelosporium* in Sturm's DEUTSCHLANDS FLORA for a fungus collected in 1827 on dead stems of *Allium* (*Amaryllidaceae*) and *Hemerocallis* (*Xanthorrhoeaceae*) and characterized by ochre spores and hyphae immersed in a gel. Subsequent authors, however, overlooked the presence of the gelatinous matrix reported by Corda (1833). *Chromelosporium* has had a confusing history due to similarities of conidiogenesis found in *Hyphelia* Fr., *Ostracoderma* Fr., and *Glischroderma* Fuckel.

Juel (1920) noted that the conidiogenesis in collections of *Hyphelia terrestris* Fr. and in a fungus that he collected on soil in Mösseberg in western

Gotland, Sweden, considered to represent *Ostracoderma pulvinatum* Fr., were similar. Consequently, Juel reduced *Ostracoderma* to a synonym of *Hyphelia*. No original specimen of *Ostracoderma pulvinatum*, from Fries or Juel, were found in the S herbarium, impeding attempts to confirm whether the peridium described by Fries for *Ostracoderma* as “peridio rotundato minime villosio sed crustaceo” and the one supposedly observed by Juel (1920) are made of a definite pseudotissue of dense intricate hyphal cells enveloping the totality of the conidioma as in *Glischroderma cinctum* Fuckel or comprises just a superficial agglutination of hyphae embedded in a gel that upon drying becomes a crust-like thin layer, covering only parts of the hyphal mat—a “peridium indeterminatum e villo in pelliculam cohaerentem context,” as observed by Fries in *Hyphelia* and by Korf (1994).

Because Fries based his generic type, *Hyphelia rosea*, on “*Trichoderma roseum* Pers. (non *Trichothecium* Link),” Hughes (1958) [having identified *Trichoderma roseum* Pers. and *Trichothecium roseum* (Pers.) Link as homotypic] considered the name *Hyphelia* no longer available. Therefore, Hughes (1958) rejected Juel’s synonymy and, following Juel’s observations, adopted *Ostracoderma* for species with similar conidiogenesis, such as *Hyphelia terrestris* and *Chromelosporium ochraceum*, making *Chromelosporium* a synonym of *Ostracoderma*. Hennebert (1973) segregated the non-peridiate *Chromelosporium* (with *C. ochraceum* and other species) from the peridiate *Ostracoderma* and *Glischroderma*.

Korf (1994) reported several *Chromelosporium*-like specimens from soil and litter in New York State with a superficial gelatinous mass, which he placed in *Glischroderma*, a genus described by Fuckel in 1870 and characterized by a superficial sticky gel (*glischros* = viscous). Norman and Egger (1999) sequenced one of Korf’s anamorphs and demonstrated that it was affiliated with the *Pachyphlodes*–*Plicariella* [as *Scabropezia*] lineage. In examining Korf’s specimens identified as *Glischroderma*, Healy (2015) recognized additional epigeous anamorphs of *Pachyphlodes* species and molecularly linked *Pachyphlodes pfisteri*, a truffle with a *Chromelosporium*-like anamorph. Hennebert (2017) subsequently distinguished *Chromelosporium* from *Glischroderma*⁽¹⁾.

⁽¹⁾ The list of specimens examined under *Pachyphlodes pfisteri* in Hennebert (2017) erroneously cites specimens received on loan from CUP instead of citing specimens identified as *Pachyphlodes pfisteri* (represented by CUP 62646, 62650, 62651, 62653, 63540, 63648) based on conidial size and ornamentation and hyphal width; CUP 62652, 62654, 63647, 63695 represent undefined species.

The presence of gel embedding the conidiogenous cells in *Chromelosporium* incited the senior author to search for fresh samples for further investigations. Fourteen samples of *Chromelosporium*-like spore mats were then collected on bare or mossy soils or mixed with organic debris in forests in Belgium, some of them bearing a few gel droplets. These *Chromelosporium*-like specimens were identified by ITS barcoding as two species of *Pachyphlodes* and an undetermined species of the *Pachyphlodes*–*Plicariella* lineage. Their anamorphs are described below and compared to the type specimen and original description of *Chromelosporium ochraceum*. This comparative morphological study revealed clear distinctions from *Chromelosporium ochraceum*.

Materials & methods

SPECIMENS. Fourteen specimens were collected in the forest, accessioned, and deposited in MUCL. The type specimen of *Chromelosporium ochraceum* (A.C.J. Corda 155414) was borrowed from the Herbarium Kryptogamologicum Musei Nationalis Pragae in Prague (PRM). Microscopical examinations and drawings were carried out using a 1960 phase contrast Olympus FH microscope equipped with a Wild drawing tube. The photographs used in figure 6 were made with an Olympus BX50 microscope equipped with Olympus SC100 numerical camera and Olympus screen. All drawings and photographs are made from samples mounted in lactic acid with Cotton blue.

SEQUENCING. DNA was extracted from fragments of five freshly collected samples in lysis buffer, using innuPREP Plant DNA kit following the manufacturer's recommendations. Sequences were determined for the nuc rDNA ITS1–5.8S–ITS2 region (ITS) with the primer pair ITS5 and ITS4 (White & al. 1990). PCR conditions are as described in Gordillo & Decock (2018). Amplicons were sequenced in both directions by Macrogen Inc. (Korea) using the same primers. MK prefixes designate sequences deposited in GenBank.

Taxonomy

Anamorph of *Pachyphlodes nemoralis* Hobart, Bóna & A. Paz,

Ascomycetes.org. 7(6):363, 2015

FIGS 1, 6A

HYPHAL MATS forming cushion-shaped or flattened patches, irregular in outline, grouped, 3–23 mm in diam., 1–3 mm high, white when young discoloring to pale yellow ochre when mature, the surface appearing fluffy to compacted, with a few superficial, small droplets of translucent, glutinous, liquid gel, drying orange and flattened, small, brittle crust-like, the margin remaining fluffy and powdery.

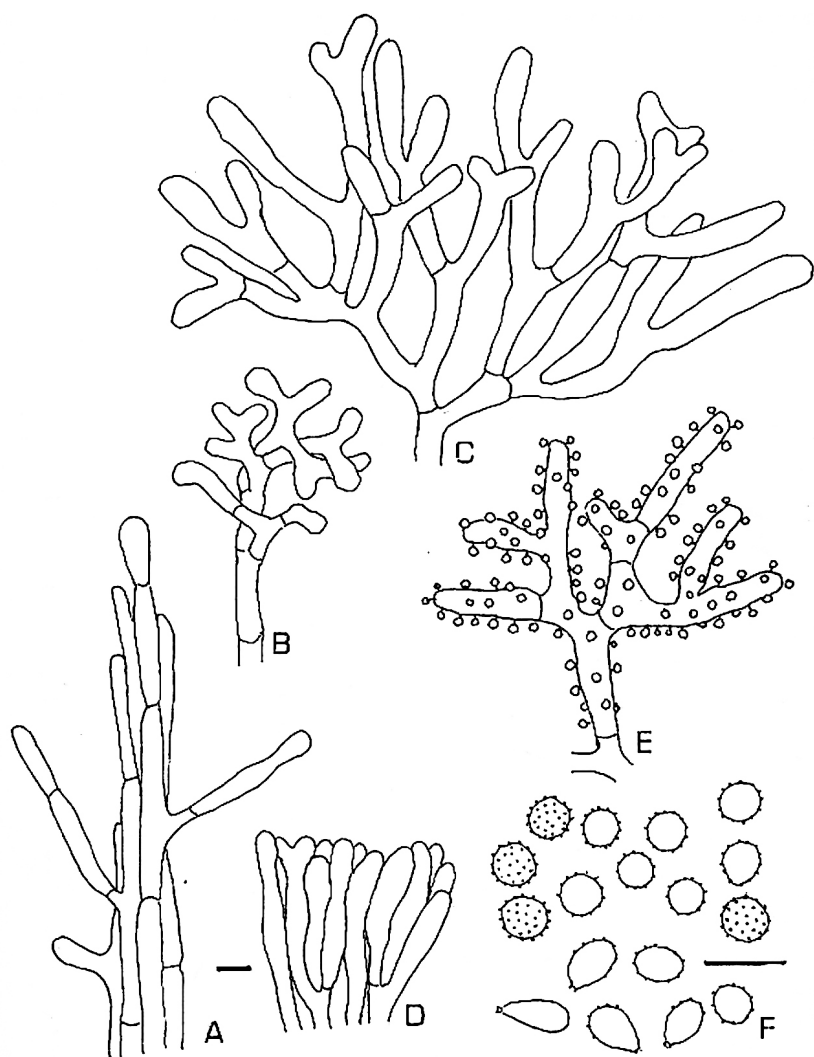


FIG. 1. *Pachyphlodes nemoralis* anamorph (MUCL 56524).
 A. Synnema. B. Young branching. C. Open branching. D. Compact terminal cells.
 E. Conidiogenous branches. F. Conidia (Scale bars = 10 μ m).

HYPHAE at first loosely interwoven, smooth, hyaline, 4–8 μm diam., becoming fasciculate, forming hyaline, erect synnemata ≤ 35 μm diam., made of hyphae with 2–20 septa, with lateral branches at wide angles, all hyphae turning into apically branched conidiogenous cells, with a repeated asymmetrical bifurcating pattern, coralloid, at variable angles, openly disposed to very compact, sparsely septate, each branch 15–50 μm long, and ≤ 10 μm diam. at the inflated apical section, covered at maturity along their entire length with conidia.

CONIDIOGENESIS holoblastic, more or less synchronous with minute denticles, 1–2 μm long.

CONIDIA globose to subglobose, hyaline, 4–6.5 μm , averaging ~ 5 μm diam. excluding warts, rarely ovoid or pyriform in moist conditions, 4×6.5 (–8) μm , the wall cyanophilic, 0.5 μm thick, warted or tuberculate all over, warts, ≤ 0.3 μm high, evenly-spaced, 12–14 in median section.

HABITAT. On soil, moss, and organic debris along paths under *Quercus* and *Fagus sylvatica* trees in forest.

SPECIMENS EXAMINED: BELGIUM, WALLOON BRABANT, Ottignies-LLN, Lauzelle forest, on soil, moss, and organic debris along paths under *Quercus* and *Fagus sylvatica*, October 2017, coll. GL Hennebert (MUCL 56520, GenBank MK714923; MUCL 56524, GenBank MK714924; MUCL 56529, GenBank MK71492).

Anamorph of *Pachyphlodes citrina* (Berk. & Broome) Doweld,

Index Fungorum 31: 1, 2013

FIGS 2, 6B

HYPHAL MATS forming cushion-shaped or flattened patches, irregular in outline, somewhat in groups, 2–25 mm in diam., 1–2 mm high, white when young, discoloring to pale yellow ochre when mature, with a dense surface and fluffy margin, the largest patches bearing superficially droplets of translucent, glutinous, liquid gel, becoming orange flattened crust-like and brittle when dried.

HYPHAE at first loosely interwoven and branched, smooth, hyaline, 3–6 (–8) μm diam., with 2–15 septa, becoming fasciculate in hyaline, erect synnemata, ≤ 25 μm wide, the hyphae frequently anastomosed, laterally and apically branched, furcating repeatedly and asymmetrically, sparsely septate, each part 10–25 μm long and terminally inflated ≤ 8 μm wide, covered at maturity all along their length with conidia.

CONIDIOGENESIS holoblastic, more or less synchronous with minute, denticles, 1 μm long.

CONIDIA globose to subglobose, hyaline, pale yellow ochre in mass, 4.5–7 μm , averaging ~ 5.2 μm diam., excluding warts, with a cyanophilic

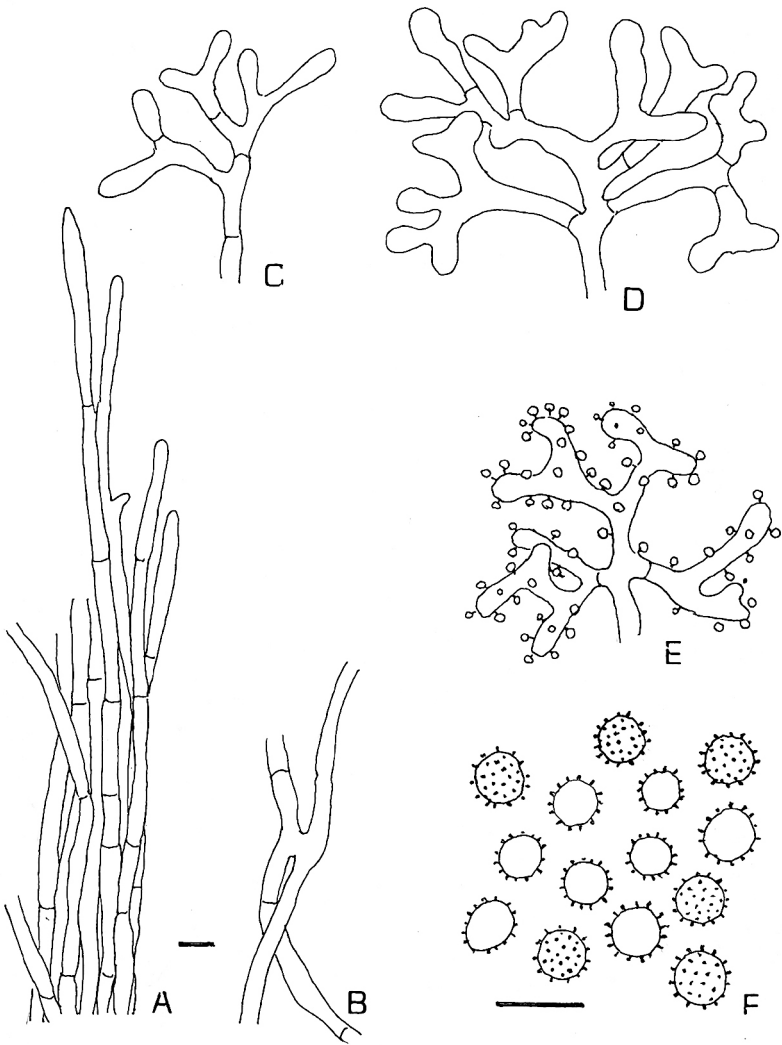


FIG. 2. *Pachyphlodes citrina* anamorph (MUCL 56652). A. Synnema. B. Anastomosis. C. Young branching. D. Developed branches. E. Conidiogenous branches. F. Conidia (Scale bars = 10 µm).

wall 0.5 μm thick, coarsely warted or baculate all over, warts cylindrical, apically blunt, ≤ 0.8 μm high, evenly spaced, 12–14 in median view.

HABITAT. On soil along path near *Castanea* and *Larix* in forest.

SPECIMEN EXAMINED: BELGIUM, WALLOON BRABANT, Ottignies-LLN, Lauzelle Forest, on soil along path near *Castanea* and *Larix* in Lauzelle forest, October 2017, coll. GL Hennebert (MUCL 56652, GenBank MK714926).

Anamorph of undetermined *Plicariella* sp. or *Pachyphlodes* sp. FIGS 3, 6C

HYPHAL MATS forming cushion-shaped patches, determinate, irregular in outline, grouped, 1–5 mm in diam., 1–2 mm high, white when young to yellow ochre in color when mature, with surface fluffy to compacted and granulose, a few fresh mature patches bearing a droplet of translucent glutinous gel, forming a local orange flattened brittle crust when dried, the margin, if not the entire patch, remaining fluffy and granulose.

HYPHAE at first loosely interwoven, smooth, hyaline, 3–7 μm diam., 2–10-septate, becoming fasciculate in hyaline erect synnemata ≤ 20 μm wide, becoming terminally branched through repeated and asymmetric bifurcations to form coralloid branch tips that are openly disposed or compacted and sparsely septate. Each part of branch is 10–70 μm long and inflated ≤ 8 μm , covered at maturity all along their length with conidia.

CONIDIOGENESIS holoblastic more or less synchronous with minute denticles 1–1.5 μm long.

CONIDIA globose, hyaline, (3–)3.5–4.5 μm , most 4 μm diam., with a finely punctate wall.

HABITAT. Soil, moss, and organic debris along path under mixed trees in forest.

SPECIMEN EXAMINED: BELGIUM, WALLOON BRABANT, Ottignies-LLN, Lauzelle forest, on soil along path in, October 2017, coll. GL Hennebert (MUCL 56522, GenBank MK714927).

Original descriptions by Corda (1833)

Chromelosporium Corda and *C. ochraceum* Corda, Sturm's Deutschlands Flora.

Abbildungen nach Natur., Abt. III Die Pilze, Bd. 3, p. 81, Tab. 41, 1833.

“CHROMELOSPORIUM Corda

Char. Gen. Sporae continuae coloratae, in gelatinae nidulantes, floccis heterogeneis destructis ramosis, articulatis, hyalinis inspersae. Acervuli effuse colorati.

[Gen. char. Spores simple, colored, embedded in gel, hyphae dispersed, hyaline, heterogeneous, articulate, branches fragmented; mats extended, colored.]

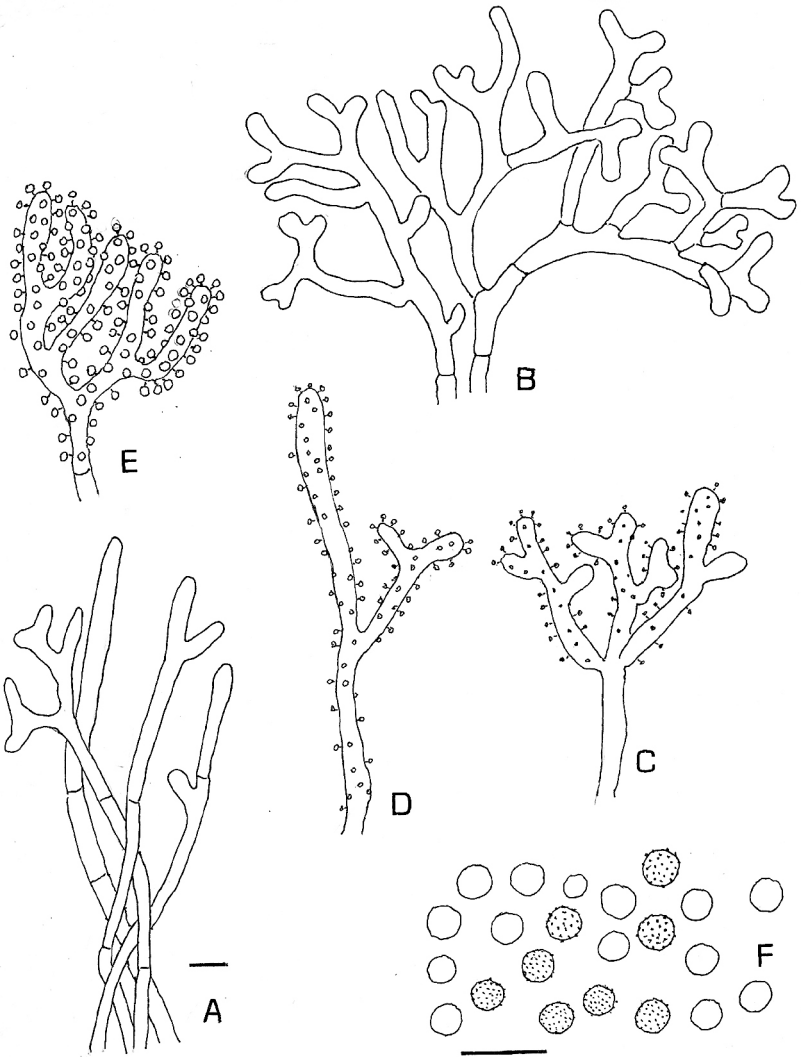


FIG. 3. *Plicariella* sp. or *Pachyphlodes* sp. anamorph (MUCL 56522).
A. Tip of synnema, B. Branching, C–E Conidiogenous hyphae. F. Conidia. (Scale bars = 10 μ m).

CHROMELOSPORIUM OCHRACEUM Corda

Ocherfärbige Chromelosporie. Tab. 41

Ch. acervulis effusis ochraceis pulverulentis; sporis copiosissimis globosis ochraceis, gelatinae coloratae immersis; floccis hyalinis grosse-articulatis albis.

[Fungus cushion-like, effuse, ochre in color, pulverulent; spores very abundant, globose, ochre in color, immersed in a colored gel, dispersed in hyphae hyaline, white, branched and broadly articulate.]

Chr. mit verbreiteten ocherfärbigen, bestäubten Häufchen, sehr häufigen ocherfärbigen, mit gefärbten Schleim eingehüllten, kuglichen Sporen, und durchsichtigen, weissen, grossgegliederten Fäden.

Wohnt auf faulenden Stengeln der Liliaceen, vorzüglich der *Hemerocallis* und *Allium*, 1827.

Die grossgegliederten, und nicht durch Scheidewände (septa) getheilten Fäden unterscheiden diese Gattung von *Sporotrichum*, so wie auch die gefärbten Sporen, da *Sporotrichum* flocci septati (non articulati) und sporae homogeneae besitzt.

Die glashellen, weissen, grossgliedrigen, niederliegenden und verworrenen Fäden, sind wenig ästig, und im Vergleich zu ihren Sporen sehr gross und sparsam.

Die Sporen selbst sind nicht aus den Fäden entstanden, daher heterogen, sind kuglich, klein, sehr zahlreich, intensive ocherfarb, fast ziegelroth gefärbt. Die sind einfach, und nicht getheilt, auch sind sie durch einen im Wasser leicht löslichen und gefärbten Schleim Häufchenartig an die Fäden befestigt.

[Ch. in extended, ochre, powdery mats, very often covered by a colored gel, spores globose, hyphae hyaline, in broad segments.

Habitat on rotten stems of *Liliaceae*, such as *Hemerocallis* and *Allium*. 1827.

The articulate and not septate hyphae distinguish this genus from *Sporotrichum*, which also has colored spores, septate hyphae and homogeneous spores.

The hyphae are hyaline, articulate, prostrate, interwoven, sparsely branched and, compared to the spores, broad and sparse.

The spores themselves are not formed from the hyphae, thus heterogeneous. They are globose, small, very abundant, deep ochre, near reddish colored. They are simple, not septate; they are also fixed to the hyphae forming a kind of head by the colored gel slightly dissolved in water]

Tab. 41. A. Natürliche Grösse. B. Fäden mit Sporen. C. Sporen noch stärker vergrössert. A. J. Corda."

CORDA'S SECOND GENERIC DESCRIPTION (1842)

In *ICONES FUNGORUM HUIUSQUE COGNITORUM*, V, p. 8, Prague 1842, Corda gives a shortened description of *Chromelosporium* with a new comment:



PLATE 4. *Chromelosporium ochraceum* Corda,
Sturm's Deutschl. Fl., III (Pilze), 3(13): 81, tab. 41, 1833

“**CHROMELOSPORIUM** Corda, Sturm Fl. III, 13, p. 81.

Sporae continuae, coloratae, gelatinae immersae, floccis heterogeneis, articulatis, repentibus, ramosis, hyalinis inspersae.

K. Wir haben eine deutliche Schleimmasse gefunden, welche die Sporen und Flocken einhüllte.”

[Spores simple, colored, embedded in gel, among hyphae heterogeneous, articulate, prostrate, branched, hyaline.

COMMENTS. We have found a conspicuous mass of gel covering the spores and hyphae.]

Chromelosporium ochraceum re-examined

Chromelosporium ochraceum Corda,

Sturm's Deutschl. Fl., III (Pilze), 3(13): 81, tab. 41, 1833.

FIGS 5, 6D

HOLOTYPE: Czechoslovakia, Prague, “*Chromelotrichum*[crossed out]*sporium ochraceum* Ca. ramulis furcis, *Myrinema* generis” [scr. & del. A.C.J. Corda]. On *Allium* dead stem. (Herb. Corda in PRM 155414).

COLONIES in small patches ≤ 10 mm, velvety, at first white then ochraceous when sporulating, made of two layers, one of conidiophores under one of terminal conidiogenous branches.

CONIDIOPHORES erect, mononematous, emerging from creeping hyphae, 3–5 μm diam. in the substratum, made of a bulbous basal cell, 28–35 $\times$ 12–15 μm , ochraceous, extending into a cylindrical, septate stipe, 100–400 μm long, light to ochraceous, the individual cells 40–95 $\times$ 10–14 μm , repeatedly branched, terminating with up to five dichotomous branches, each branch most often with a basal septum, and a second one next to the subsequent dichotomous branches, their length decreasing from one dichotomy to the next, usually the first basal dichotomy 40–90 $\times$ 9–10 μm , the second 30–70 $\times$ 6–10 μm , the third 30–50 $\times$ 6–9 μm , but in some cases dichotomies very short, decreasing from 20–10 μm , the range of angles in the dichotomies from 35–45°.

CONIDIGENOUS CELLS comprising up to four terminal dichotomies, together 70–100 $\times$ 6–9 μm , often apically clavate to 11 μm diam., bearing conidia all along with small, denticles 2 $\times$ 1 μm , collapsing after conidial release, seceding at their basal septum, rarely leaving a frill on the last conidiophore cell.

CONIDIA holoblastic, borne singly on denticles, at maturity globose or subglobose, thick-walled, cyanophilic, verrucose, ochraceous to salmon in mass, 4–5.5 μm diam., ≤ 6 μm including warts, warts prominent and blunt, 12–18 in median view.

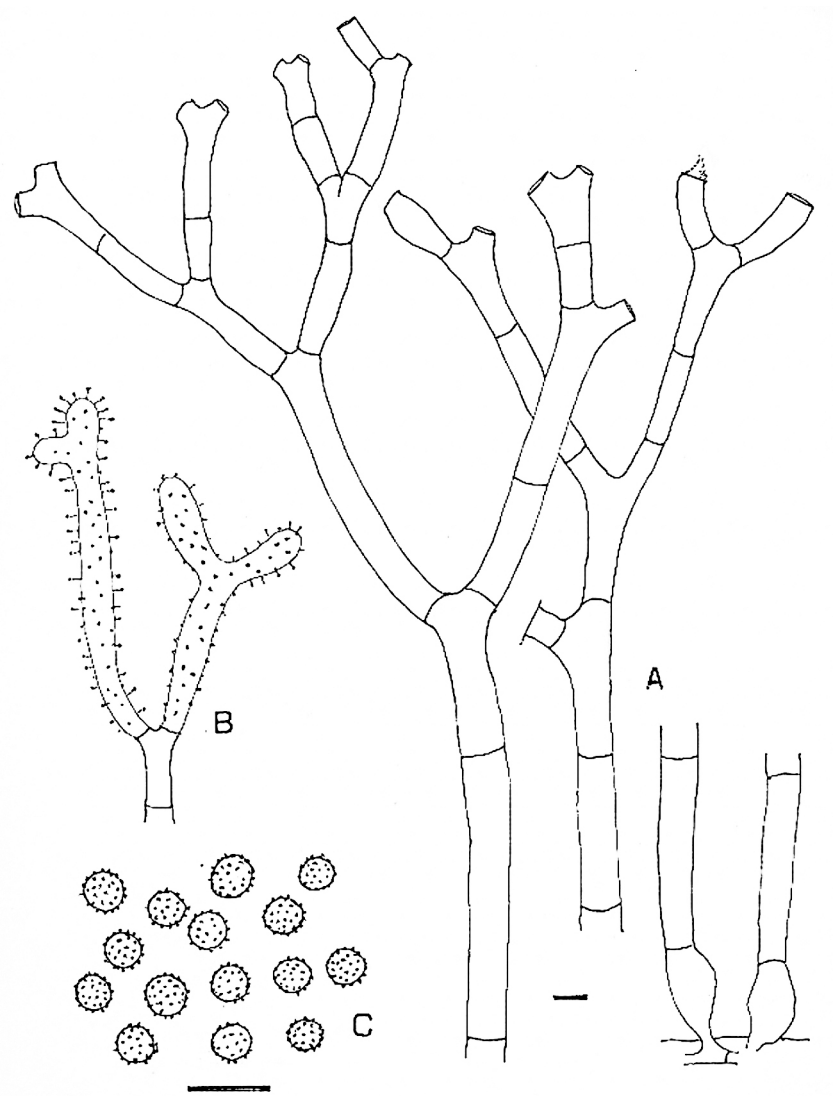


FIG. 5. *Chromelosporium ochraceum* Corda (Holotype PR 155414). A. Conidiophores stipes with basal cell and dichotomous branching. B. Terminal conidiogenous dichotomies. C. conidia (Scale bars = 10 μ m).

COMMENTS—The terms used by Corda interpreting his observations illustrated in FIG. 4 (Corda's fig. 41b) may raise some questions. The hyphae described as broadly articulate (“grosse-articulatis, grossegegliederten”) appear in the figure to be hyphae distantly septate in long cells, drawn in their natural dichotomous position. Also the “ramis destructis” might refer to collapsed and disappeared conidiogenous branches after conidial release. That would explain why Corda did not report attachments of the conidia to hyphae, which he said were heterogeneous (“floccis heterogeneis, sporen nicht aus den Fäden entstanden, daher heterogen”). The gel reported as colored (“gelatinae coloratae, gefärbten Schleim”), is translucent and may appear colored because of the embedded ochre spores. Our observations suggest that Corda noted those characters from an over-mature collection.

Discussion

Corda (1833, 1842) described *Chromelosporium ochraceum* with conidia embedded in a gel. However, this character was not considered significant by Hughes (1958) or Hennebert (1973) until Korf (1994) collected *Chromelosporium*-like specimens with a superficial gel and Healy (2015) noticed gel on anamorphic growth of *Pachyphlodes* spore-mats when crushed.

The gel, if noticed on fresh anamorphs in humid conditions, may appear on dried herbarium specimens as an orange spot, membranous and brittle, variable in size (as small as 2 mm) or may leave no traces, as is the case for the type specimen of *Chromelosporium ochraceum*. After the very dry summer of 2017, we observed gel droplets on only a few samples in shady places. In our opinion, the presence of gel is not a reliable, stable character, and its degree of development is probably circumstantial and dependent on environmental conditions.

The anamorphs of *P. nemoralis* and *P. citrina* are not yet described (R. Healy, pers. comm.). The anamorph of *Pachyphlodes pfisteri* Tocci & al., an endemic North American taxon, was described and illustrated with macro- and micro-photographs by Healy & al. (2015) and drawn by Hennebert (2017). Its conidiogenesis is in all respects identical to that of *P. nemoralis* and *P. citrina* (FIGS 1, 2).

The anamorphs of the two *Pachyphlodes* and one undetermined *Pachyphlodes*–*Plicariella* species here described show distinctive features, particularly in hyphal width, conidiophore branching, and conidial size and ornamentation (FIG. 6). These characters should be examined in more *Pachyphlodes* and *Plicariella* species to evaluate their diagnostic value.

Although they have the same type of conidiogenesis, *Chromelosporium ochraceum*, the generic type species, differs significantly from *Pachyphlodes* and *Plicariella* in its anamorphic morphology. *Chromelosporium*, as demonstrated by *C. ochraceum*, has mononematous, erect apically branched conidiophores with regular dichotomies, each branch delimited by a septum, with up to four terminal dichotomies bearing holoblastic, synchronous conidia. *Pachyphlodes* and *Pachyphlodes-Plicariella* as shown here differ from *Chromelosporium* by creeping and erect, intermixed synnematous conidiophores, with lateral and apical coralloid branches that are sparsely septate and bearing holoblastic synchronous conidia along the entire length.

Conclusion

Differences found here between the anamorphs of *Pachyphlodes* species and the *Pachyphlodes-Plicariella* lineage and the anamorphs and the type species of *Chromelosporium* include synnematous versus mononematous conidiophores, apical and lateral branching versus solely apical branching, and spore production along most branches of the spore mat versus being limited to terminal hyphal branches. These differences might provide morphological evidence for maintaining *Chromelosporium* as a distinct genus from *Pachyphlodes*.

It remains to compare the morphologies of the still unknown anamorphs of *P. ligerica* (Tul. & C. Tul) Zobel, the type species of *Pachyphlodes* Zobel, and of *Plicariella radula* (Berk. & Broome) Rehm, the type species of *Plicariella* (Sacc.) Rehm, with the description provided here for *C. ochraceum* to confirm the morphological distinctiveness of the anamorphs of these lineages. The most expedient solution to answering the question of relatedness would be molecular analyses of *C. ochraceum* in its fresh anamorphic and/or sexual phases (yet to be discovered) and of the types of *Pachyphlodes* and *Plicariella*.

Another group of species presently named in *Chromelosporium*, *C. coerulescens* (Bonord.) Hennebert and *C. carneum* (Pers.) Hennebert, do not produce gel but form erect synnematous conidiophores, coralloid branching, and similar conidiogenesis (Hennebert 1973). These appear to be morphologically closer to the anamorphs of *Pachyphlodes-Plicariella* than to *Chromelosporium*. Genetic analysis should decide their taxonomic position in the *Pezizaceae*.

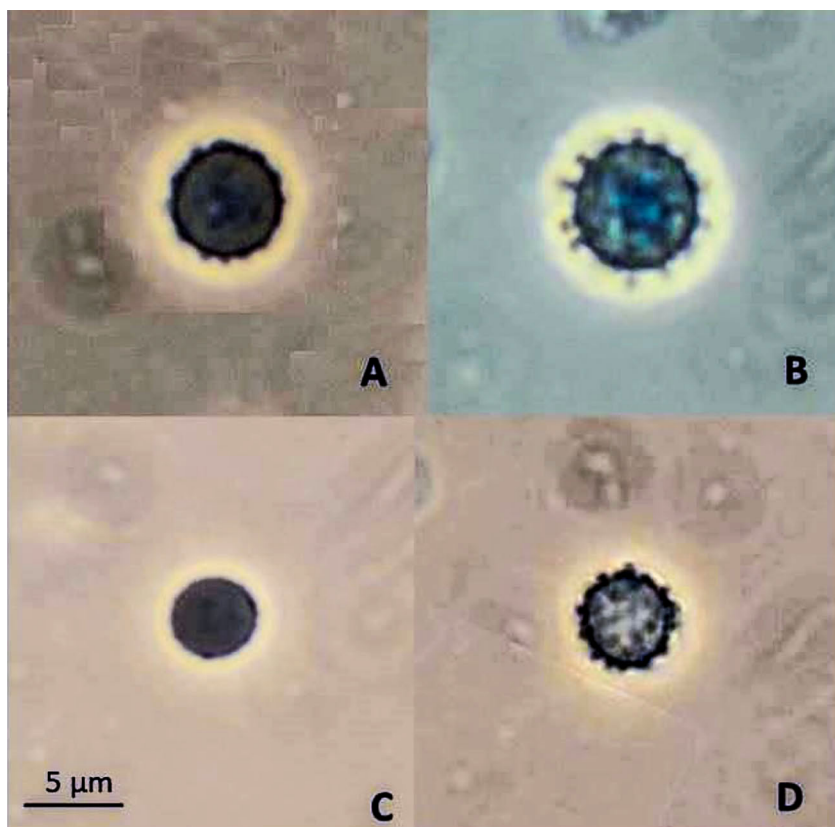


PLATE. 6. Conidial ornamentation: A. *Pachyphlodes nemoralis* (MUCL 56524). B. *P. citrina* (MUCL 56652). C. *Plicariella* sp. or *Pachyphlodes* sp. (MUCL 56522). D. *Chromelosporium ochraceum* (Type PR 155414).

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